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Age dependent costs of reproduction in a sexually dimorphic species

- Male fallow deer as an example

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Master's thesis
Grimsö 2017

Independent project/Degree project / SLU, Department of Ecology 2017:15

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Credits: 30 HEC
Level: A2E
Course title: Degree project in Biology – Master's thesis
Course code: EX0565
Place of publication: Grimsö
Year of publication: 2017
Cover picture: Martin Sundström
Title of series: Independent project/Degree project / SLU, Department of Ecology
Part number: 2017:15
Online publication: http://stud.epsilon.slu.se

Keywords: *Dama dama,* cost of reproduction, home range size, sexual dimorphism

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Abstract

Energy and time are two of the most important factors limiting the investment spent on reproduction for an organism. Due to this limitation, individuals have to balance between using energy for maintenance or growth and using it for reproduction. In many polygynous male mammals, reproduction has been pointed out to be the most energetically costly time of the year and in sexually size dimorphic species mortality is sex-biased toward the larger sex. Fallow deer is a polygynous, seasonally breeding species demonstrating a high level of sexual size dimorphism where males can be double the size of females. During the breeding season, males compete for females and display on the breeding site. Behaviours like fighting, vocalization and a reduction in forage intake can be very costly and males often loose a large amount of weight.

In this study, I estimate the cost of reproduction by using culling data together with movement data collected from wild GPS-marked male fallow deer. I compare timing of body mass- and bone marrow fat loss with daily average movements and home range sizes between different age classes during time of rut. Mature males (≥ 4-years-old) lost on average 24% of their body mass during pre- and post-rut and had a decline in bone marrow fat of approx. 20%. Simultaneously, younger males (≤ 2-years-old) lost much less, if anything. Additionally, males 1 – 2-years-old had the highest mobility during rut while 4 year- and older ones moved least. There were no significant differences in home range sizes between mature and immature males and of all seasons was autumn the season with largest home range sizes, highly influenced by the time of rut. These results suggest that the loss in body mass is not due to a higher mobility during rut and the distinct decline in both body mass and bone marrow fat indicates a large investment into reproduction in mature males. Finally, as far as I know, there are no previous published studies ever of male fallow deer home range sizes, based on GPS-data, making this study unique from that perspective.

Keywords: *Dama dama*, fallow deer, cost of reproduction, home range size, sexual dimorphism

Populärvetenskaplig sammanfattning

Tid och energi är två av de viktigaste faktorerna vilka begränsar en organisms möjlighet att reproducera sig. På grund av denna begränsning tvingas individerna balansera sin energiförbrukning mellan att använda den för överlevnad och kroppstillväxt eller till reproduktion. Parningstiden eller brunsten har pekats ut som den mest energikrävande perioden på året hos hanar som parar sig med många honor (polygami). Hos arter där graden av polygami är hög – dvs då vissa hanar parar sig med väldigt många honor och andra inte lyckas para sig alls, är det ofta även stor skillnad i storlek mellan könen. Kanske på grund av den höga konkurrensen om parningar och dödligheten i anslutning till brunsten är då ofta riktad mot det större könet.

Dovhjort är en polygam art vilken förökar sig under en specifik period på året. I Sverige inträffar högbrunsten oftast i oktober. Hos arten finns en tydlig storleksskillnad mellan könen, så kallad könsdimorfi, där hanarna kan bli dubbelt så stora som honorna. Under parningssäsongen tävlar hanarna mot varandra och visar upp sig på specifika parningsområden kallade brunstplatser. Den starkaste och mest dominanta hanen är den som får para sig med flest honor. Beteenden som slagsmål, brölande och minskat födointag tycks vara väldigt kostsamma och hanar tappar ofta mycket vikt under brunstperioden. En på året sen brunst, den kraftiga viktnedgången och en mycket begränsad tid för fysisk återhämtning innan kommande vinter kan vara förödande och i värsta fall leda till döden.

I den här studien uppskattar jag den fysiologiska kostnaden för brunsten genom att använda avskjutningsdata tillsammans med rörelsedata från GPS-märkta, vilda, dovhjortar. Datat är insamlad på Koberg egendoms marker i Västergötland under nio år (2006 – 2015). Brunsten definierades här på individnivå via de GPS-märkta handjuren till den period då de gick till- respektive lämnade sin brunstplats. Under åren 2007 – 2011 inföll brunsten på Koberg i genomsnitt 27 september till 8 november, med variationen 15 dagar för vardera början och slut. Genomsnittligen både startade och avslutade de yngre hanarna (2 år) brunsten senare än de äldre hanarna (≥ 3 år).

Handjurens viktnedgång och förändringar i halten benmärgsfett jämförs i tid med förändringen i daglig genomsnittlig förflyttning och djurens hemområdesstorlek för olika åldersgrupper under brunstperioden. De yngsta handjuren, 1 – 2 år gamla, rörde sig mest under brunsten medan de äldre hanarna, 4 år och äldre, rörde sig minst. Trots detta tappade de äldre handjuren (≥ 4 år) i genomsnitt 24% av sin kroppsvikt under brunsten och förlorade cirka 20% benmärgsfett. Under samma period tappade de yngre hanarna (≤ 2 år) inte alls lika mycket, om ens något. Däremot hittades inga statistiskt signifikanta skillnader i hemområdesstorlekar mellan äldre och yngre handjur. Under hösten var hemområdesstorlekarna som störst, vilket var starkt påverkat av brunstperioden. Dessa resultat antyder att viktnedgången inte beror på att de vuxna hjortarna rör sig mer under brunsten utan avmagring och sjunkande benmärgsfett tyder på att de äldre hanarna lägger stora resurser på parningen och sannolikt inte kompenserar detta med ett ökat födointag. Slutligen, vad jag vet finns inga tidigare publicerade studier på dovhjortshanars hemområdesstorlekar baserade på GPS-data, vilket gör denna studie unik ur det perspektivet.

Nyckelord: *Dama dama*, dovhjort, kostnad för reproduktion, hemområdesstorlek, könsdimorfism

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1 Introduction

In evolutionary theory, a fundamental part is about trade-offs between different life history variables. One important trade-off is the cost of reproduction where individuals have to balance between for example increased current fecundity and a reduction in future reproduction (Reznick, 1985) or the allocation of energy between somatic growth and reproduction (Stephens et al., 2009).

Energy and time are two of the most important factors limiting the investment spent on reproduction for an organism. Costs of reproduction are usually described as either ethological- or physiological costs. The ethological costs correspond to the behavioural act of reproduction. Individuals are for example increasing their exposure to predators during the mating season in general and during the act of copulation in particular, or during the following parental care of the young. The physiological costs are due to the individual using energy that could have been used for maintenance or growth, instead using it for reproduction (Jönsson, 1991). Two of the most designated examples of physiological reproductive costs are gestation and particularly lactation (Clutton-brock et al., 1983; Sand, 1998) which requires a lot of energy from mammalian females (Gittleman and Thompson, 1988).

In many polygynous male mammals the most energetically costly part of the year have been pointed out to be the reproduction (Reindeer: Leaderwilliams and Ricketts, 1982; Squirrel: Michener and Locklear, 1990; Red deer: Clutton-Brock et al., 1982; Yoccoz et al., 2002; elephant seal: Galimberti et al., 2007) In species where the level of polygyny is high there is often also a high size dimorphism between sexes due to the competition over mates (Loison et al., 1999; Andersson, 1994). Males that compete for females and do have any kind of display on the breeding site often loose a large amount of weight during breeding season (Andersson, 1994). Sexual dimorphism increases with body weight (Cluttonbrock et al., 1977) and do have a significant relation to sex-biased mortality (Promislow, 1992). In species where males are bigger than females, mortality is male-biased (Promislow, 1992).

In male ungulates as in moose bulls (*Alces alces*), it has been proposed a distinctly cost to participate in the rut due to the appetite suppression, hypophagia (Miquelle, 1990). Red deer (*Cervus elaphus*) males do reduce their time feeding by 90 % during harem holding and they lose up to 20% of their body weight (Clutton-Brock et al., 1982). Mass loss and reduction in forage intake during breeding season have also been observed in fallow deer (*Dama dama*) (Apollonio and Di Vittorio, 2004) where mature males (5 - 8 years old) lost on average circa 26% of their body mass during the breeding season (McElligott et al., 2003). The animals rely on stored fat reserves during the rut, the same reserve that also is needed to cope with limited food supply during winter (Miquelle, 1990).

Fallow deer is a seasonally breeding species (Chapman and Chapman, 1970), they are polygynous and there is a high level of sexual size dimorphism (McElligott et al., 2001). The time of rut, or mating season, is in fallow deer males associated with behaviors like fighting (McElligott and Hayden, 2000), vocalization (McElligott et al., 1999), reduction in forage intake, hypophagia, (Apollonio and Di Vittorio, 2004) and scraping of rutting pits (Stenstrom et al., 2000) which males scent urinate (Apollonio et al., 1989). Many territorial males fight (Willisch et al., 2015) which can lead to serious injuries, breaking of antlers and in worst case males being killed (Apollonio et al., 1989; McElligott and Hayden, 2000). Well before the rut males arrive to the breeding sites for starting with their marking activities. Older males usually arrive earlier than younger ones (Ciuti and Apollonio, 2016). Groaning happens first,

then hypophagia and scent-urination (Apollonio and Di Vittorio, 2004). Most of the dominance status are disclosed already before males start to vocalise (McElligott et al., 2003), partly in the bachelor groups (McElligott et al., 1998). In fallow deer males there is a high mortality before the age of four, indicating a strong selection even before they reach the age of social maturity (McElligott and Hayden, 2000). Higher ranked males start vocalize earlier than lower ranked ones and is typically vocal for more days (McElligott et al., 1999).

Fallow deer males use different mating systems and can change strategy during a rut season (Moore et al., 1995). The variation in mating strategies have been related to the energy costs of defending females and/or resources (SanJose and Braza, 1997). Territorial males are usually at least 5 years old and typically not older than 8 years. So called *followers* are mainly younger or older than territorial males (Moore et al., 1995). Age, dominance and mating strategy are things that most often influence mating success (Moore et al., 1995). The majority of matings are achieved by 5 - 8 year old males (McElligott and Hayden, 2000; Moore et al., 1995) and of those it is mainly the high ranked who gain matings (Farrell et al., 2011; Komers et al., 1997).

The spatial configuration of the landscape, habitat requirements and mating system have been pointed out as important factors influencing home range size in ungulates (Bevanda et al., 2015; Ofstad et al., 2016). The amount of food and nutrition offered by the area should be enough to support the requirements of the individual´s daily needs (Ciuti et al., 2011). During rut, territorial male fallow deer defend an area that offers high values in resources (e.g. food and shelter) valuable for females. When resources declines males have been seen to switch mating tactic to a follower tactic, instead chasing females (Moore et al., 1995). Annual home range sizes have been supposed to be highly influenced by the behaviour of males during breeding season (Borkowski and Pudelko, 2007; Davini et al., 2004). Surprisingly, to my knowledge, there are no previous studies on home range sizes of male fallow deer based on GPS-data. Data from earlier studies where home range and habitat use have been surveyed have mainly been collected during day time by direct observations in field (Putman, 1986) and with a small sample of VHF-marked animals (3 males by Borkowski and Pudelko, 2007; 7 enclosed males by Davini et al., 2004; 19 males by Nugent, 1994). Borkowski and Pudelko (2007) suggested that when individuals do move in open habitats, as in the case with fallow deer, it may not be enough to only use daytime data when looking at habitat use of animals. Hence, if possible it is preferred to use 24-hour data. In this study, I will analyse home rage sizes and daily movements of wild male fallow deer by using GPS-data which offers a greater overall picture with 24 hour-data.

1.1 Aims of the study

The aim of this study is to quantify age specific costs of reproduction in wild fallow deer males. I will do this by using culling data from male fallow deer collected during nine hunting years (2006 - 2015) on the approx. 90 km^2 Koberg estate, in south western Sweden. Measures of body mass and relative bone marrow fat content from males of different ages will be used to investigate annual variation patterns in relation to time of rut. Also, I will use data from 28 GPS-collared fallow deer males from the same study area to investigate age specific timing of the rut by analysing changes in movement patterns during the year and finally if such changes coincide with weight loss. The GPS-data will also be used to calculate annual and seasonal home range sizes in different age classes of males.

1.2 Predictions

Energy in mammals is primarily stored in form of adipose tissue (Lindstedt and Boyce, 1985) and the marrow fat content typically decline during winter (Ballard, 1995). I thus predict that (1) decreasing bone marrow fat content coinciding with the rut indicates a cost of reproduction and (2) a quantitative difference in bone marrow fat content between mature and young males as a consequence of their investment in the rut (Ciuti and Apollonio, 2016).

Former studies on fallow deer, and other male ungulates (e.g. moose and red deer) indicating a sharp decline in body mass as a consequence of the contribution in the rut (Apollonio and Di Vittorio, 2004; Clutton-Brock et al., 1982; Miquelle, 1990) Based on that I do predict (3) a decline in body mass during the time of rut for the males in this study. Also, younger males do not invest as much in the rut as the older ones (Ciuti and Apollonio, 2016) thus I predict, (4) a difference in mass loss between young (< 4 yrs.) and mature (≥ 4 yrs.) males.

Non-territorial males typically have a high mobility during mating season compared to the territorial ones (Ciuti et al., 2011). Thus, I also predict (5) a higher daily average movement (DAM) distance indicating higher mobility and finally, (6) larger home range sizes (movement over larger areas) of the young males compared to the older ones. If this is true while the older males are the only age class that lose body mass and fat, this will strengthen the hypothesis of an age dependent cost of reproduction by hypophagia (Apollonio and Di Vittorio, 2004) and a consequent increased risk of mortality due to starvation during the following winter.

2 Materials and Methods

2.1 Study site and population

Data for this study was collected from killed fallow deer males in a wild population at Koberg estate (58ºN, 12ºE), Västra Götaland county in south western Sweden. Free ranging fallow deer has been present in the area since the end of 1920's (Silfverschiöld, unpublished data). The estate does comprise 90 km^2 of land whereof 54.35 km^2 are included by the study area. The area mainly consists of different types of forests (79%) and arable land and pastures (16%). The latter is primarily cultivated to improve wildlife habitats (i.e. deer grazing) (Winsa, 2008). A fenced road (country road 42) divide the area in two parts where the northern part is the smaller one (~30 km^2) and the southern part the larger (~60 km^2). The northern part is also the one holding the lower density (114.3 fallow deer/10 km^2) compared to the southern part (307.7 fallow deer/10 km^2) (Kjellander, unpublished data). To maintain the high density of fallow deer in the area the animals get supplementary feed during the winter and cropped pastures served as game field (Grönberg, 2011).

2.2 Movement data

A dataset with GPS-positions from 28 fallow deer males with data collected during five years (2006 - 2011) were used for investigate time of rut. Males were supplied with GPS-collars (Vectronic Aerospace GmbH, Berlin, Germany, model Pro-light) programed to take a position every fourth hour. Since I wanted to investigate age specific start and end of rut period,

individuals were divided into different age classes. Birth was set to 1 of June. Some individuals wore the GPS-collar during several years and will thus occur in several age classes at different years and corrected for statistically by treating ID as a random factor when necessary.

2.2.1 Time of rut

Time of rut was defined with Net Square Displacement (NSD) analysis (Börger and Fryxell, 2012). If NSDs showed a change in movement pattern during autumn the beginning of the change was set to start of rut for that individual. When the movement went back to "normal" that was set to end (for NSD-plots, see appendix 1). Individuals who travelled into breeding areas, the date leaving its ordinary home range was set to start of rut and the date leaving breeding area was set to end of rut.

In total, 59 individual NSDs were performed of which 26 had location data that reached over a whole autumn and could be used for identifying start- and/or end date of rut for each individual and year. In 25 cases a start date could be identified and in 15 a clear date defining the end. In some of the cases males stayed at the rut area over the winter (n = 4), making it hard to find a clear end date. There were also cases where individuals lost their collar or the GPS-transmitter stopped working (n = 3) or individuals that died (n = 4) during rut. Finally, there was one case where the start of rut could not be found. This was because the individual was marked at the rutting site during time of rut.

2.2.2 Home range size

Analyses of annual home rages were based on individuals with location data for ≥ 9 month of a year. For analysis of seasonal home ranges the limitation was set to ≥ 50 locations per season. In roe deer, even ≤ 40 locations have been suggested to be sufficient to define over 90% of the whole winter home range area and ≥ 45 for 100% (Guillet, 1994). Also, individual should have locations collected during ≥ 50% of the season.

In total, there were data collected from 28 GPS-collared male fallow deer. After dividing individuals into different age classes this resulted in 59 age specific annual home ranges where some males were represented in several age classes. Out of these 59 home ranges, only eight represented a whole year. An additional of three individuals had data collected from ≥ 9 months. Two individuals dispersed during GPS-monitoring, and thus removed from the analysis of home range size. This resulting in a total of nine individuals that was used for analyses of yearly home rage sizes. Only one individual (ID-14) was represented in two different age classes.

Annual home range sizes were calculated both with the defined rut included and excluded. When calculating home ranges with rut excluded were coordinates between dates of rut, analysed with NSD removed.

GPS-data from 28 individuals divided by age and season generated 153 age specific seasonal home ranges. After removing individuals with < 50 locations/season (n = 19) and those with data from < 50% of a given season (n = 23) there were 111 seasons left that could be analysed for seasonal home range sizes. Also, two additional seasons were removed because the individuals dispersed during that time. Out of the 109 remaining seasons there were 21 autumns, 26 summers, 31 winters and 31 springs. Seasons were divided as follows;

summer: 1 June – 31 August, autumn: 1 September – 14 December, winter: 15 December – 31 March, spring: 1 April – 31 May.

2.2.3 Daily average movement

The daily average movement was calculated for every individual and age to investigate how long distances individuals move during a day. The distances were calculated using Pythagoras theorem between coordinates and then taking mean distance per day. Individuals were divided into three age groups; 1-2-year-olds, 3-year-olds and 4 year and older ones.

2.3 Culling data

Data-sets of culling data were used for analysis of weight loss and bone marrow fat. The data-set mainly included data from animals being shot during hunting season (1st of September – 28th of February). Complementary data and data collected before and after hunting season could for example be from animals culled on special permits, animals found sick and on that account put to death, animals killed in vehicle incidents or individuals found dead for unknown reason.

Weight data (total body mass, dressed weight and slaughter weight) and length of metatarsus from fallow deer males collected during nine hunting years (2006 - 2015) was used for analysis of weight loss. Measures of dry- and wet weight of bone marrow fat taken from jaws was collected from year 2012 to 2015 and used for analysis of relative bone marrow fat.

A relative date (1 - 365) was created to define when each individual was killed by setting first of July to day 1**.** The individuals were divided into following age groups: calves (0-year old), yearlings (1-year), stags (2-year old) and mature males (≥ 4-year old). Three-year-old males were omitted from most analysis because of the large variation in the level of maturation in this age group (n = 19).

2.3.1 Relative body mass and bone marrow fat

To correct for size a relative body mass (kg) for individuals was calculated by dividing dressed weight with length of the hind foot i.e. metatarsus length (cm). Dressed weight is here defined by the whole body, skin, head and legs after removing all guts, intestines, organs, heart and lungs. In total 1810 animals was used for calculations of relative body mass, whereof 1755 had data of dressed weight. In the cases were the dressed weight was missing a conversion factor was used together with either slaughter weight (n = 28) or total body mass (n = 27) to calculate a standardized dress weight. Different conversion factor for each of the age classes was used. Conversion factors for slaughter weight was as follows; calves: 1.38, yearlings: 1.34, 2-year olds: 1.30, ≥ 4-year olds: 1.47 and for total body mass; calves: 1.42, yearlings: 1.39, 2-year olds: 1.35, ≥ 4-year olds: 1.36.

Relative bone marrow fat content extracted from the jaw bone (lower mandible) was used as a measure of current condition of each individual. Low bone marrow fat content would indicate that the animal is near starvation or in bad condition (Ballard, 1995). Jaws from animals killed in the study area have been systematically collected for aging since 2006 while analyses of the bone marrow fat started in 2012. The wet- and dry weight of the bone marrow is weighted at lab and used for calculations of relative bone marrow fat % (dry

weight/wet weight) after drying for ≥ 7 days. Individuals were divided into two age classes: young (1 - 2 years old) and mature (≥ 4 years old). There were only four individuals with the age of three year and were thus excluded from further analysis due to a too small sample.

2.4 Statistics and analysis

All analysis in the study were performed in Rstudio (Version 0.99.473 – © 2009-2015 RStudio, Inc). For all work and processing with the GPS-data, ArcGIS (ArcMap 10.2.2.3552 – © 2009-2014 Esri) was used to look at home ranges and movements on a map.

Data for weight loss during rut was analysed using generalized additive models (GAM) with smooth terms. Since some individuals were represented in several ages in the GPS-data, a generalized additive mixed model (GAMM) with id as a random factor was used for the daily average movement to correct for pseudo replicates. To find the most parsimonious model Akaike Information Criterion corrected for small sample sizes (AICc) was used (Burnham and Anderson, 2002). AIC do compare different explanatory models and deals with the trade-off between the goodness of fit and the complexity of the model (number of parameters), telling which model is the simplest one that explain the data best (Burnham and Anderson, 2002).

Annual and seasonal home range sizes were calculated in the package AdehabitatHR using 95% Minimum Convex Polygon (MCP). Same dataset as which was used for analyses for time of rut was utilised. For analysing differences in annual home range size between the two age-groups the Welch two sample t-test was used. Data were a bit right-skewed and therefore log transformed before the test was made. When comparing seasonal home range sizes an analysis of covariance (ANCOVA) was used to test for differences in home range size between both age classes and seasons. This data was right-shewed as well and therefore log transformed. A Tukeys's HSD (honest significant difference) test was used to find out between what seasons a significant difference in size occurred. Individual home range sizes, both seasonal and annual, as well as net squared displacement (NSD) were analysed with package AdehabitatLT.

3 Results

3.1 Time of rut

Based on NSD, the earliest identified individual date for start of rut took place the 14th of August 2010 and the latest at 18th October 2008. The earliest individual date for end of rut was identified as 11th of October 2008 and the latest at 15th of December 2007. When all age classes were included, this gives a mean start date of rut at 27th of September (± 14.6 days) and a mean end date at 8th of November (± 15.2 days). All extreme (earliest and latest) stops and starts of rut, were performed by including two- and three-year-old individuals. In general, three-year-olds and older males both started and ended rut earlier than younger males (Table 1). Mean peak of rut, when including all males, was at October 18.

Table 1. Start and stop dates of rut for different age classes of wild fallow deer males at Koberg estate, Sweden based on net squared displacement analyses (NSD). GPS-data was collected between the years 2007 - 2011. Because some individuals did wear the collar for more than one year, those are represented in several age classes. "First" and "last" represent the earliest and the latest date an individual started and ended rut according on NSD in respective age class. Total is the time of rut for all individuals and age groups together.

Age	Start		End	
	Mean (first/last)	n	Mean (first/last)	n
2	8 Oct (29 Sep/18 Oct)	4	17 Nov (9 Nov/15 Dec)	3
3	25 Sep (14 Aug/13 Oct)	6	6 Nov (11 Oct/1 Dec)	3
4+	25 Sep (29 Aug/15 Oct)	15	5 Nov (4 Nov/12 Nov)	9
Total	27 Sep (14 Aug/18 Oct)	25	8 Nov (11 Oct/15 Dec)	15

3.2 Home range size

A total of nine individuals were used for calculations of annual home range sizes. Seven of the individuals had their rutting area within the annual home range area and two (ID-1 and ID-549) leaved "home" and traveled into breeding areas at another place. Consequently, when rut was included those two had the biggest home ranges (Table 2). Mean annual home range size when all individuals were included was 2.7 km^2 when rut was excluded and 6.5 km^2 when rut was included. Removing the two individuals who travelled into breeding areas during time of rut, when rut is included, mean instead was 4.2 km^2 with no significant difference between the two age-groups. Neither when rut was included (t-test, $t = -0.18$; $p = 0.86$; $df = 5.50$), nor when rut was excluded (t-test, $t = 0.24$; $p = 0.82$; $df = 4.74$).

Table 2. Annual and individual home range size, (km^2, 95% MCP) for fallow deer males at Koberg estate, Sweden. Data collected by wild GPS-collared males during five years (2006 - 2011). Mean sizes for two different age-classes (±SD). Animal ID-1 and ID-549 leaved "home" and travelled into breeding areas during time of rut.

Animal-ID	Age	Home rage size (km^2)	
		Rut included	Rut excluded
1	2	17.6	2.1
553	2	3.4	2.6
558	2	2.9	2.0
14	3	5.2	2.8
14	4	4.8	2.4
563	4	2.9	1.8
549	5	11.5	2.5
15	7	7.3	6.6
25	11	2.7	1.4
Mean subadult	2-3	7.3 (± 7.0)	2.4 (± 0.4)
Mean adult	≥ 4	5.8 (± 3.7)	2.9 (± 2.1)

For analysis of seasonal home range size there were data used from 25 males and 109 seasons. No significantly differences were found between age groups ($p = 0.23$). However, there were

a significant difference between seasons ($p < 0.001$) where autumn significantly differed from all other seasons. Also, winter and summer significantly differed from each other. Autumn was the season when males had largest home range sizes (mean = 7.7 km^2) while spring and summer were smallest (mean = 1.9 km^2 and 1.3 km^2, respectively; Table 3).

Table 3. Seasonal home range sizes (km^2) for different age classes of male fallow deer at Koberg estate, Sweden, based on 25 individuals and 109 seasons. Data collected by wild GPS-collared males during five years (2006 - 2011). "min" and "max" stands for the smallest and the largest home range in respective age class. "n" is the number of seasons with calculated home ranges during respective season. Some individuals are represented in several age classes.

Age group	Autumn		Summer		Winter		Spring	
	mean (min - max)	n	mean (min - max)	n	mean (min - max)	n	mean (min - max)	n
1-2	7.4 (3.4 - 15.0)	3	1.0 (0.5 – 1.3)	4	2.7 (0.8 – 8.0)	11	2.4 (1.0 – 8.4)	13
3	9.6 (3.7 - 23.3)	4	2.0 (0.8 – 5.6)	7	3.6 (0.6 – 8.5)	7	1.3 (0.4 – 2.1)	6
4+	7.2 (1.2 - 22.6)	14	1.1 (0.3 – 3.5)	15	2.0 (0.6 – 5.1)	13	1.7 (0.6 – 3.9)	12
Total	7.7 (1.2 – 23.3)	21	1.3 (0.3 – 5.6)	26	2.6 (0.6 – 8.5)	31	1.9 (0.4 – 8.4)	31

3.3 Daily average movement

For analysis of daily average movement (DAM), a total of 10162 days allocated into three age groups were used (1 - 2 yrs.: 3053 days, 3 yrs.: 2080 days, ≥ 4 yrs.: 5029 days). There was a significant difference in DAM between all age groups where younger males had the highest movement and older males the lowest ($p < 0.001$). Also, DAM significantly differed over time for all age groups (GAMM: $R^2 = 0.129$; approximate significance of smooth terms for all age groups: $p < 0.001$; Figure 1).

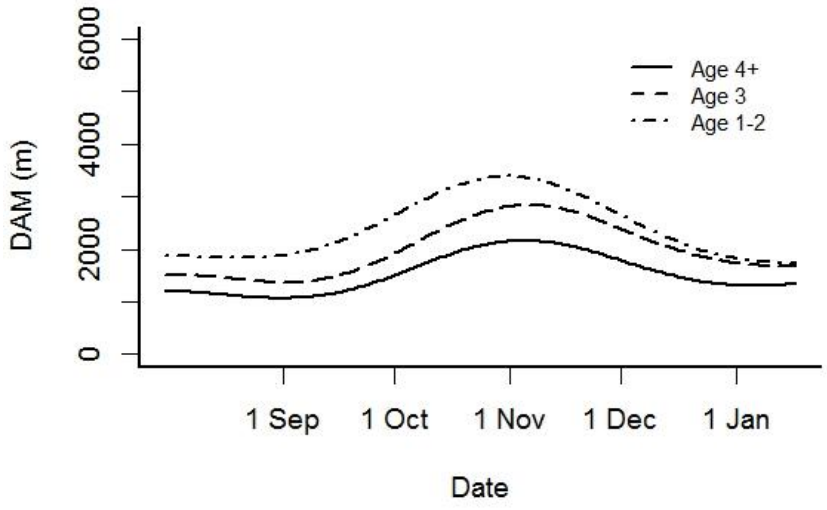

Figure 1. Daily average movement for different age groups based on a GAMM-analysis (expected values) and total 10162 days. Data collected by wild GPS-collared male fallow deer during five years (2006 - 2011) at Koberg estate, Sweden.

3.4 Relative body mass

In total, data from 1810 dead fallow deer males were used for analysis of variation in relative body mass, whereof 1255 calves (0-year old), 367 yearlings (1-year), 56 stags (2-year-old) and 132 mature males (≥ 4-year-old). The heaviest male in the dataset was 5 years old, had a dressed weight of 108 kilos and a total measured body mass of 133 kilos.

Mature males (here defined as ≥ 4-year-old) were those losing most weight during breeding season (Figure 2). Between mean rutting dates (27 Sep – 8 Nov) defined by NSD mature males lost 24.5% of their body weight and 44.2% between total rutting dates (14 Aug – 15 Dec). Two-year-olds gained 2.5% during mean rutting dates and lost 1.8% during total rutting dates. Looking at weight loss in the two age groups during mean and total time of rut, estimated separately for the age groups, mature males lost 23% during mean dates (25 Sep – 5 Nov) and 32% during total dates (29 Aug – 12 Nov). Two-year-olds lost 2% of their weight during their mean dates (8 Oct – 17 Nov) and 12% during their total dates (29 Sep – 15 Dec) of rut (Figure 3).

The most parsimonious model explaining relative body mass variation in male fallow deer was based on time (relative date) and age-class (GAM: $R^2 = 0.933$; approximate significance of smooth term for age-class 4+: $P < 0.001$; Figure 2).

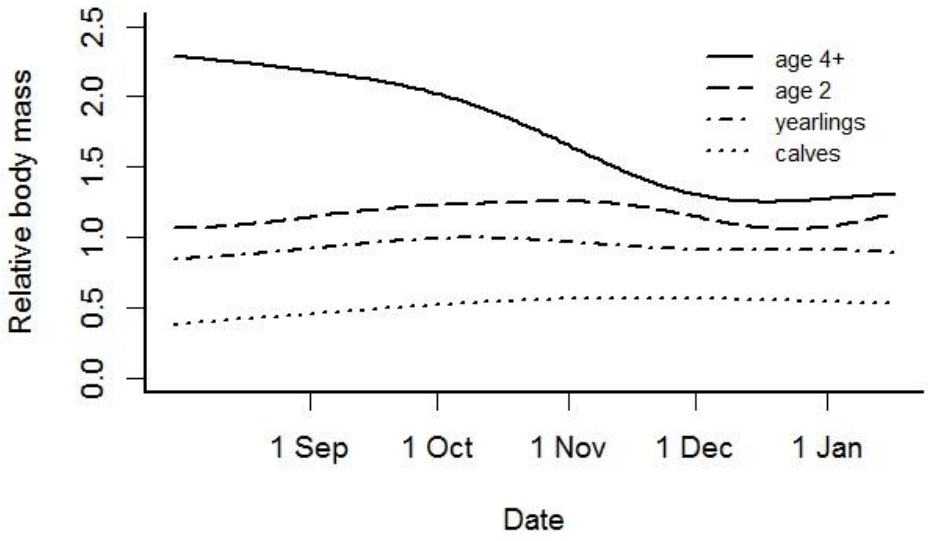

Figure 2. Relative body mass (dressed weight (kg)/metatarsus length (cm)) of male fallow deer at Koberg estate, Sweden, based on a GAM-analysis (expected values). In total, data from 1810 dead fallow deer males were used whereof 1255 calves (0-year old), 367 yearlings (1-year), 56 stags (2-year-old) and 132 mature males (≥ 4-year-old). Calves represent 0-year-old individuals and yearlings represent 1-year-old individuals. Three-year-old males were omitted because of the large variation in the level of maturation in this age group (n = 19).

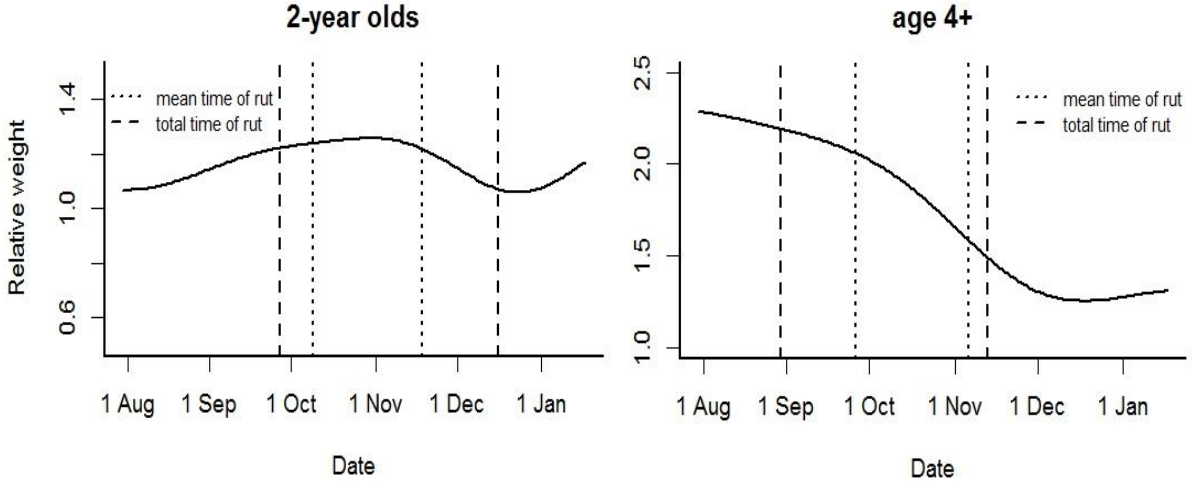

Figure 3. Weight loss during mean and total time of rut estimated from NSD of killed young males (2-year olds) and mature males (≥ 4 yrs.) at Koberg estate, Sweden. During mean time of rut mature males weigh 23% and young males 2% less compared to pre-rut-weight, respectively. During total time of rut mature males lost 32% and young males 12% of their pre-rut-weight.

3.5 Bone marrow fat

A total of 164 individuals were used for analyses of bone marrow fat, whereof 82 young (1 - 2 yrs.) and 82 mature (≥ 4 yrs.) males. No significant difference in relative bone marrow fat content (%) was found between the two age classes ($p = 0.81$), neither by time for the young males ($p = 0.21$). However, there was a significant difference in relative bone marrow fat over time in mature males (GAM: $R^2 = 0.141$; approximate significance of smooth terms $p < 0.001$; Figure 4).

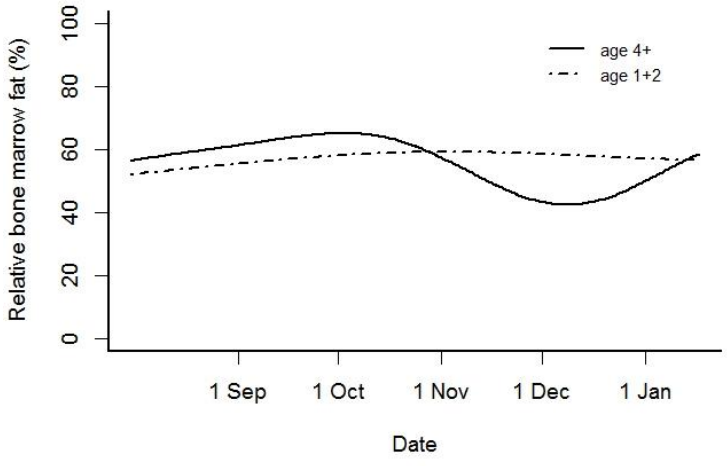

Figure 4. Relative bone marrow fat (dry weight/wet weight) in killed young males (1 – 2-year-old) and mature males (≥ 4-year-old) based on a GAM-analysis (expected values. Data collected during three years (2012-2015) at Koberg estate, Sweden.

4 Discussion

This study demonstrates in accordance with prediction 3 and 4 that older male fallow deer at Koberg (≥ 4 years) lose a large amount of their body mass during time of rut, much more than younger males (< 4 yrs.). Relative amount of bone marrow fat of mature males decline during the same time (prediction 1 and 2), while it was not determined in young one- and two-year-old males. These results support the hypothesis of an age dependent cost of reproduction in male fallow deer. The results did not support prediction 6, larger home range sizes of young males compared to older ones. However, younger males did have a higher DAM compared to mature males (prediction 5).

Studies of reproductive costs in large and long- lived animals like fallow deer can be difficult (McElligott and Hayden, 2000) as it is disproportionately time consuming, compared to many other research questions. However, there are a good number of studies where different activities that males perform during rut are studied and some alternative explanations for the weight loss have been discussed. Mating success have been related with dominance rank, age, body size (Farrell et al., 2011; McElligott et al., 2001) and mating strategy (Moore et al., 1995). However, McElligott and Hayden (2000) found that males that did mate were not significantly more likely to die following years than those that did not mate. This suggests that it is the actual participation in rut that makes males die and not the mating success per se.

4.1 Age and time of rut

Age is an important factor affecting dominance and therefore also mating success in bucks (Moore et al., 1995; Komers et al., 1997). In a study by Moore et al. (1995), no male younger than 4 years old was seen execute a successful mating and during a study lasting over twelve years Ciuti & Apollonio (2016) made the same observation. The ten most successful males accounted for over 95% of the matings each year (Moore et al., 1995). However, the fact that younger males do not mate does not mean that they are not participating in rut (Komers et al., 1997). Age itself have been pointed out to have a relatively unimportant effect on reproductive behaviour in fallow deer males (Komers et al., 1997). In the GPS-data I could see how immature males (1 – 2 yrs.) clearly changed their movement patterns during breeding season and even had a higher DAM than mature males. One two-year-old male (ID 1) left his "home" in the beginning of rut and travelled into a breeding place located some kilometres away. In the end of rut, he returned home again. Male fallow deer is coming into puberty at an age of 16 month (Chapman and Chapman, 1970) which means that they physically could proceed a successful mating already at that age. Under high competition, males at the age of 2 – 3 years are willing to participate in rut but refrain from it because they know they are not able to win a fight against dominant males (Komers et al., 1997). In populations where competition is high immature bucks invest their energy in growth rather than display, until they are old and large enough to compete with high ranked males (Birgersson and Ekvall, 1997; Pelabon and Komers, 1997). There have been suggested a "motor training function" of interactions between yearling males (≤ 2 yrs.) and females on the breeding sites. Young males interact with females learning to recognize the oestrous ones and their behaviours. This will help them get more efficient the coming breeding seasons when they are old and large enough to participate actively (Pelabon et al., 1999).

The mean peak of rut, based on NSD, for males in this study was at October 18. This agree with the peak of rut for females in this population that has been defined to be October

30, when 50% of the does have ovulated, or mean rut around October 21 based on NSD (Kindbladh 2015). Five-year-old males and older ones in this population had a mean start of rut at September 26. Ciuti and Apollonio (2016) have reported, for a fallow deer population in Italy, that older and heavier males with larger antlers moved to lekking areas about one month before the peak of rut. Moore et al. (1995) have also reported that males holding territories have been seen doing this from about three weeks before females comes into oestrus.

The mean time of rut for older males (≥ 4 yrs.) took place earlier in autumn than that for younger males (< 4 yrs.). Larger mammals have proportionality greater mass of body fat (Lindstedt and Boyce, 1985) which enables larger males to spend more time and energy on the rut. Heavier males are those losing a greater amount of body mass (McElligott et al., 2003; this study) and initial body mass have been positively related to mass loss (McElligott et al., 2003). Ciuti and Apollonio (2016) observed heavier males arriving at the lekking area earlier than lighter ones and that they also were able to defend territories for a longer time. Males 1 – 4 year old spent on average about 15 days per year in the lek area whereas the 5-year-old and older spent on average approximately 47 days per year in the lek area (Ciuti and Apollonio, 2016). No such differences in time spent on rut could be seen in my data. Days spent on rut seem to be about the same for all age classes. However, I used movement patterns analysing the time of rut and I did not observe animals and their activities in field. Territorial males have been seen having a higher mating success, and higher amount of copulations, than those who had a short-time- or no territory (Ciuti et al., 2011) and the high ranked and oldest males are those who mate earliest in rut (Farrell et al., 2011). If males are large and in good condition it seems to pay off arriving to breeding areas early and occupy the best spot. Long lek attendance has consequently been positively correlated with mating success. However, only a few males do stay at the lek for a longer time suggesting that it is costly to remain in the lek (Apollonio et al., 1989).

4.2 Home range sizes and DAM

Even though I did not observe the animals and their behaviours in my study, the loss of body mass seems not to be due to a higher mobility during rut. Younger males had the highest movement while older males were losing weight. Non-territorial males typically have a high mobility during mating season, running around between leks of dominant males (Ciuti et al., 2011). Also, there were no significant differences in home range sizes between young and old males, indicating that older males do not move over larger areas. However, there were large differences in home range size between seasons where autumn were the predominantly largest areas. When including rut in the annual home range, the size was highly influenced by this period. Males who had the largest annual home range where also among those having largest home ranges during autumn. This is in accordance with Borkowski and Pudelko (2007) that found for a fallow deer population in southern Poland and also for the one of San Rossore Preserve, Italy analysed by Davini et al. (2004). Borkowski and Pudelko (2007) reported a mean annual home range size of 9.75 km^2 and Davini et al. (2004) 5.9 km^2, both using the 95% MCP. This corresponds with sizes in my study of 7.3 km^2 for subadult males (2 – 3 yrs.) and 5.8 km^2 for adult males (≥ 4 yrs.). Nugent (1994), on the other hand, have reported an annual home range size rarely more than 3 km^2 for male fallow deer in the Blue mountains, New Zealand (100% MCP). However, in that study males were between 0 – 2 years old while males in this study were 2 – 11 years old. The home rage size of an individual largely depends

upon the amount of food and nutrition the area offers. It should be enough to support the requirements of the individual´s daily needs (Ciuti et al., 2011). During rut, territorial males defend an area that offers high values in resources (e.g. food and shelter) valuable for females. When resources declines, males have been seen to switch mating tactic to a follower tactic, and instead they start chasing females (Moore et al., 1995).

4.3 Mass loss, hypophagia and groaning

In this study, mature males (≥ 4 yrs.) lost on average 24.5% of their body mass during mean rutting dates and 44.2% between total rutting dates, reflecting a mean loss of up to 28 kg of body mass during mean rutting dates and 51 kg during total rutting dates. This is in accordance with what McElligott et al. (2003) found for the mature fallow deer males (5 - 8 years old) in a population on Ireland who lost on average circa 26% of their body mass during breeding season. In both moose and fallow deer this distinct decline in weight have been strongly associated with hypophagia (Miquelle, 1990; Apollonio and Di Vittorio, 2004). Well before the first copulation males reduce their food intake markedly. Howsoever, this reduction in food intake does not seem to be due to lack of time to feed (Apollonio and Di Vittorio, 2004; Miquelle, 1990). In a study by Apollonio and Di Vittorio (2004) they observed bucks lying down idle 60% of their time during rut. This have also been observed in moose bulls where the most common behaviours during time of rut was that bulls were standing inattentive doing nothing (Miquelle, 1990). The reduction in food intake seems more likely to be due to hormonal changes causing a loss of appetite (Apollonio and Di Vittorio, 2004). In both moose and fallow deer scent-urination and reduction in forage intake have been noted to coincide (Apollonio and Di Vittorio, 2004; Miquelle, 1990). Hypophagia could be driven by the same physiological processes as preputial gland activity and have an appetite suppressive impact (Apollonio and Di Vittorio, 2004). Another thing that have been connected to mass loss is groaning (McElligott et al., 1999) and time spent groaning have been positively associated with mating success (McElligott et al., 2003). In a study, McElligott et al. (1999) observed mature males spend up to 34% of their time during rut vocalizing. For producing a groan, it demands a lot of muscular activity and this may account for a key part of the weight lost during rut (McElligott et al., 1999). No yearlings and 2-year olds were heard groaning during a study performed by Moore et al. (1995) and only 35% of the 3-year-olds did so. Due to the fact that males stop feeding during rut, their body condition at the start of the breeding season is of fundamental importance (Apollonio et al., 1989).

Conclusions

Fallow deer breeds in late autumn and there is no time to rebuild fat reserves before winter, when many ungulates usually have an additional decline in marrow fat (Ballard, 1995). Asher et al. (1987) reported that fallow bucks don’t regain their weight until late spring and summer period and a late regain of fat reserves have also been reported for other mammal males (Michener and Locklear, 1990). For a male to participate in rut, losing a large amount of their weight and fat reserves and risk to don’t survive the coming winter, should be considered as a large cost put into the reproduction.

Acknowledgements

I want to send out a big thank to my supervisor Petter Kjellander for always take his time and help me during the process of my work with this thesis. A thank you to my second supervisor Geir Rune Rauset for a huge help with scripts in R and a first kick start with the statistics and GPS-data. Thanks also to Nadège Bonnot for further help with the statistics. Also, thanks to my examiner Håkan Sand and my student opponent Daniel Tooke for valuable criticism and aspects on this thesis. Finally, I want to send out a big thank to Anders Friberg at Koberg and the Silfverschiöld family for contributing with their land and animals and all technicians and students assisting with marking animals or taking samples of all the dead animals. Without all of you there would not be any data for this study.

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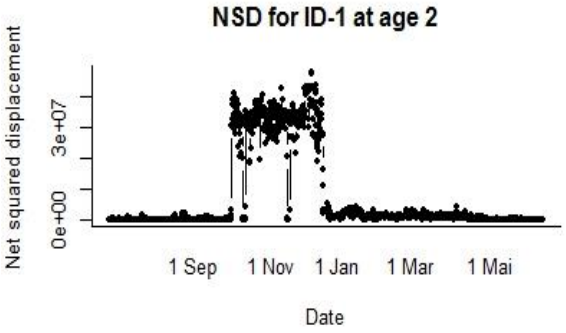
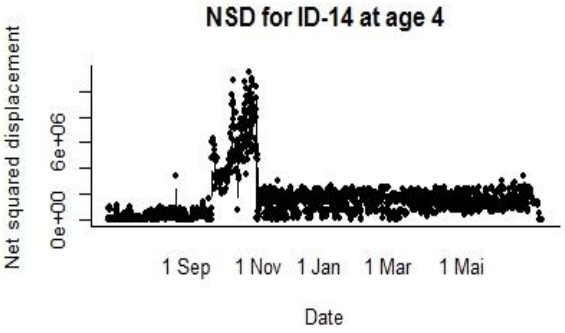
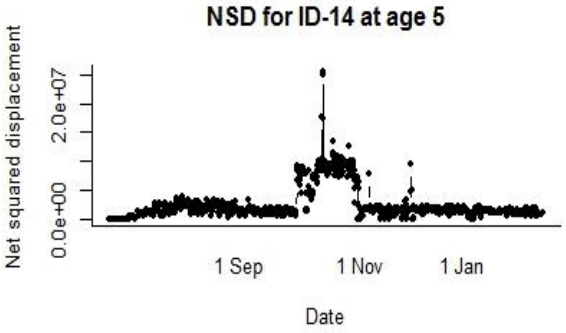
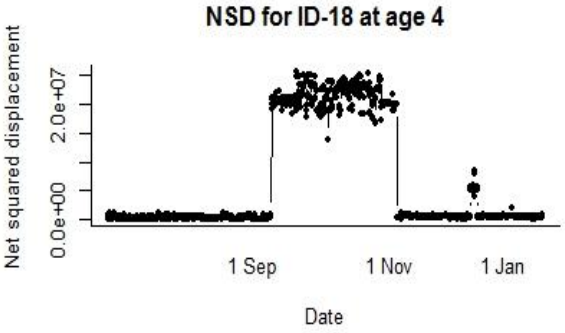
Appendices

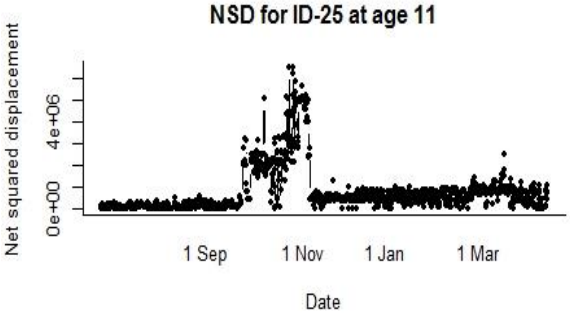
Appendix 1. NSD plots for the individual males.

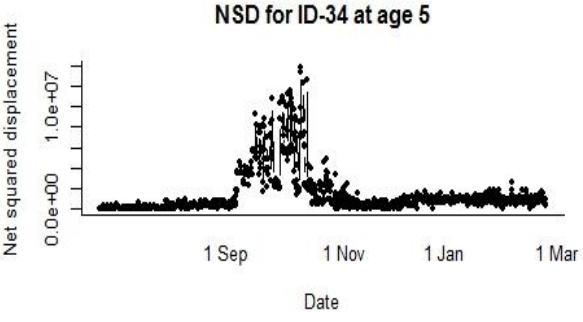


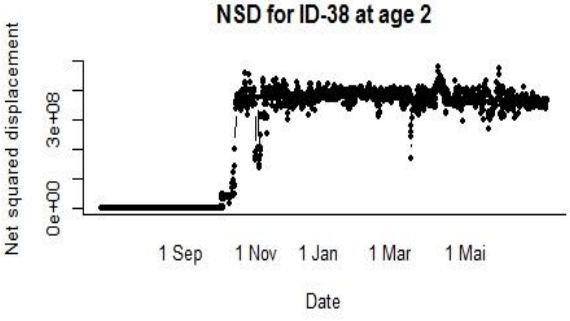


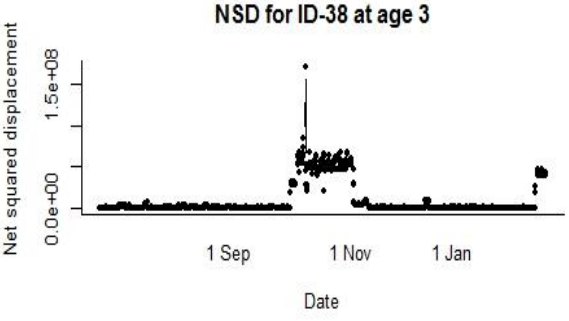


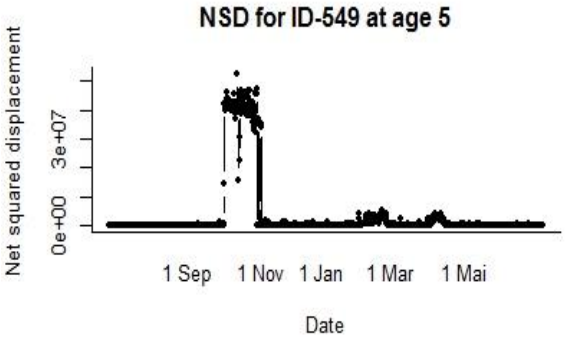


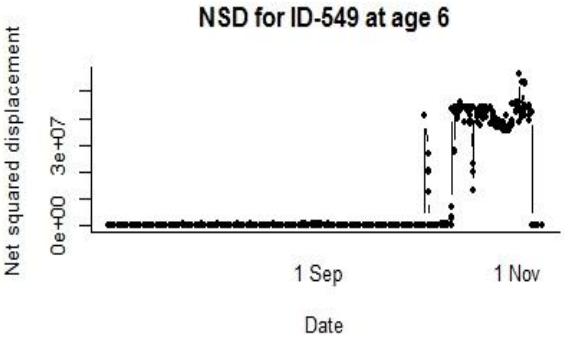


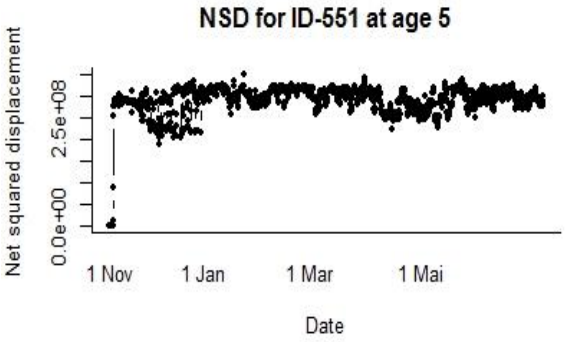


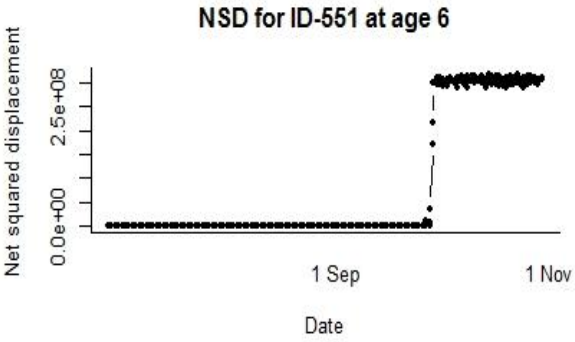


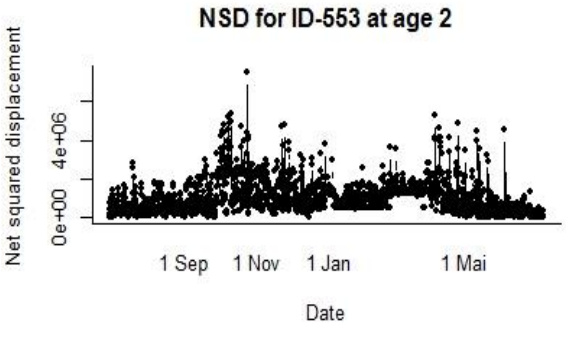


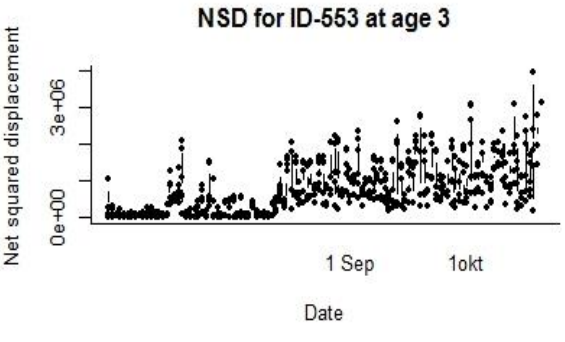

NSD for ID-549 at age 5
Net squared displacement
0e+00
3e+07
1 Sep
1 Nov
1 Jan
1 Mar
1 Mai
Date

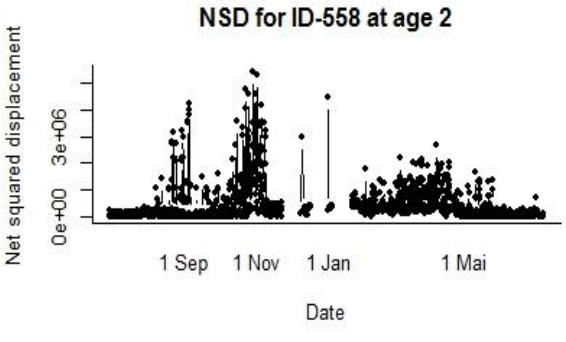

NSD for ID-549 at age 6
Net squared displacement
0e+00
3e+07
1 Sep
1 Nov
Date

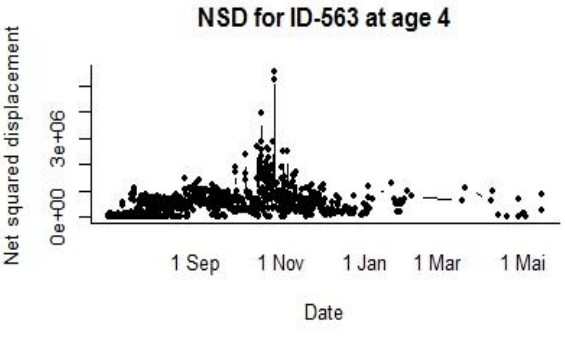

NSD for ID-551 at age 5
Net squared displacement
0.0e+00
2.5e+08
1 Nov
1 Jan
1 Mar
1 Mai
Date

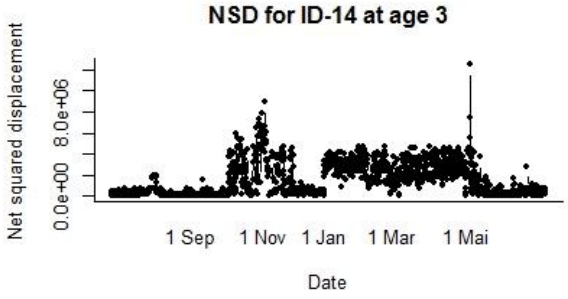

NSD for ID-551 at age 6
Net squared displacement
0.0e+00
2.5e+08
1 Sep
1 Nov
Date

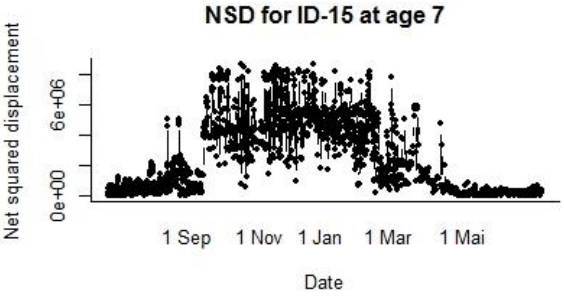

NSD for ID-553 at age 2
Net squared displacement
0e+00
4e+06
1 Sep
1 Nov
1 Jan
1 Mai
Date

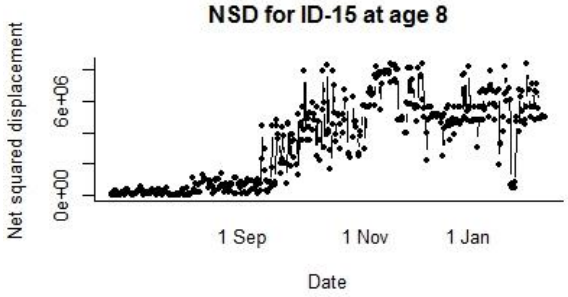

NSD for ID-553 at age 3
Net squared displacement
0e+00
3e+06
1 Sep
1okt
Date

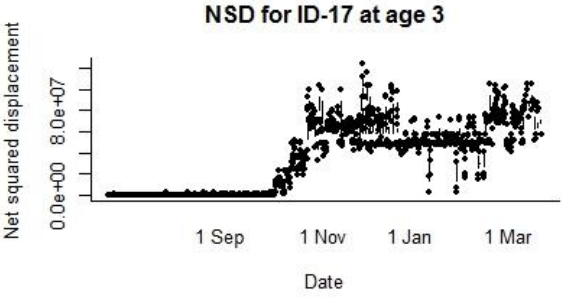

NSD for ID-558 at age 2
Net squared displacement
0e+00
3e+06
1 Sep
1 Nov
1 Jan
1 Mai
Date

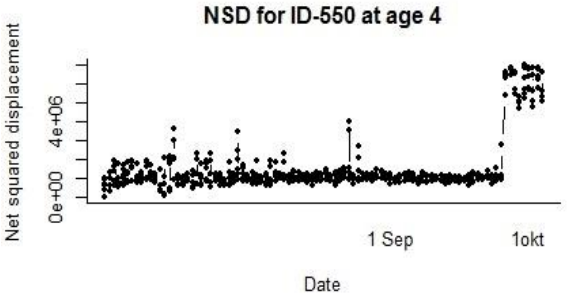

NSD for ID-563 at age 4
Net squared displacement
0e+00
3e+06
1 Sep
1 Nov
1 Jan
1 Mar
1 Mai
Date

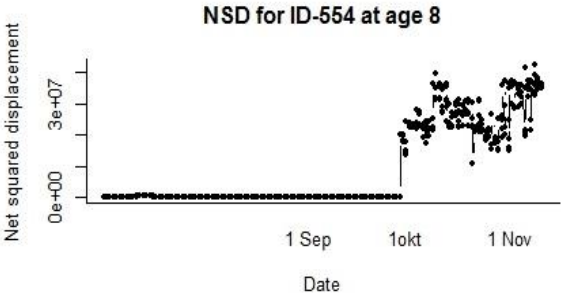

NSD for ID-14 at age 3
Net squared displacement
0.0e+00
8.0e+06
1 Sep
1 Nov
1 Jan
1 Mar
1 Mai
Date

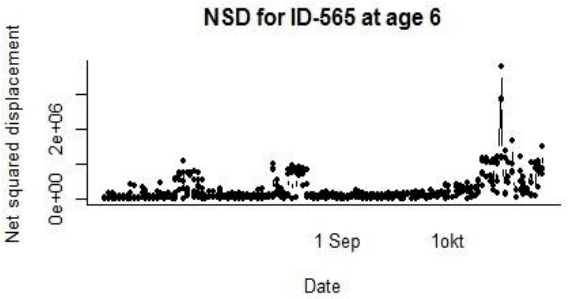

NSD for ID-15 at age 7
Net squared displacement
0e+00
6e+06
1 Sep
1 Nov
1 Jan
1 Mar
1 Mai
Date

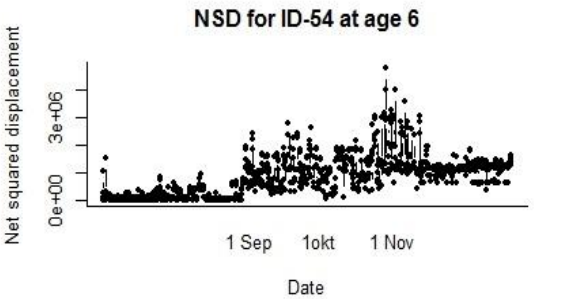

NSD for ID-15 at age 8
Net squared displacement
0e+00
6e+06
1 Sep
1 Nov
1 Jan
Date

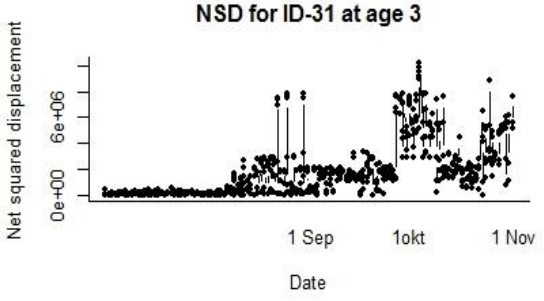

NSD for ID-17 at age 3
Net squared displacement
0.0e+00
8.0e+07
1 Sep
1 Nov
1 Jan
1 Mar
Date

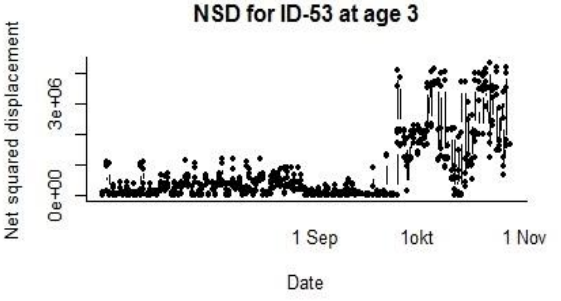

NSD for ID-550 at age 4
Net squared displacement
0e+00
4e+06
1 Sep
1okt
Date


NSD for ID-554 at age 8
Net squared displacement
0e+00
3e+07
1 Sep
1okt
1 Nov
Date

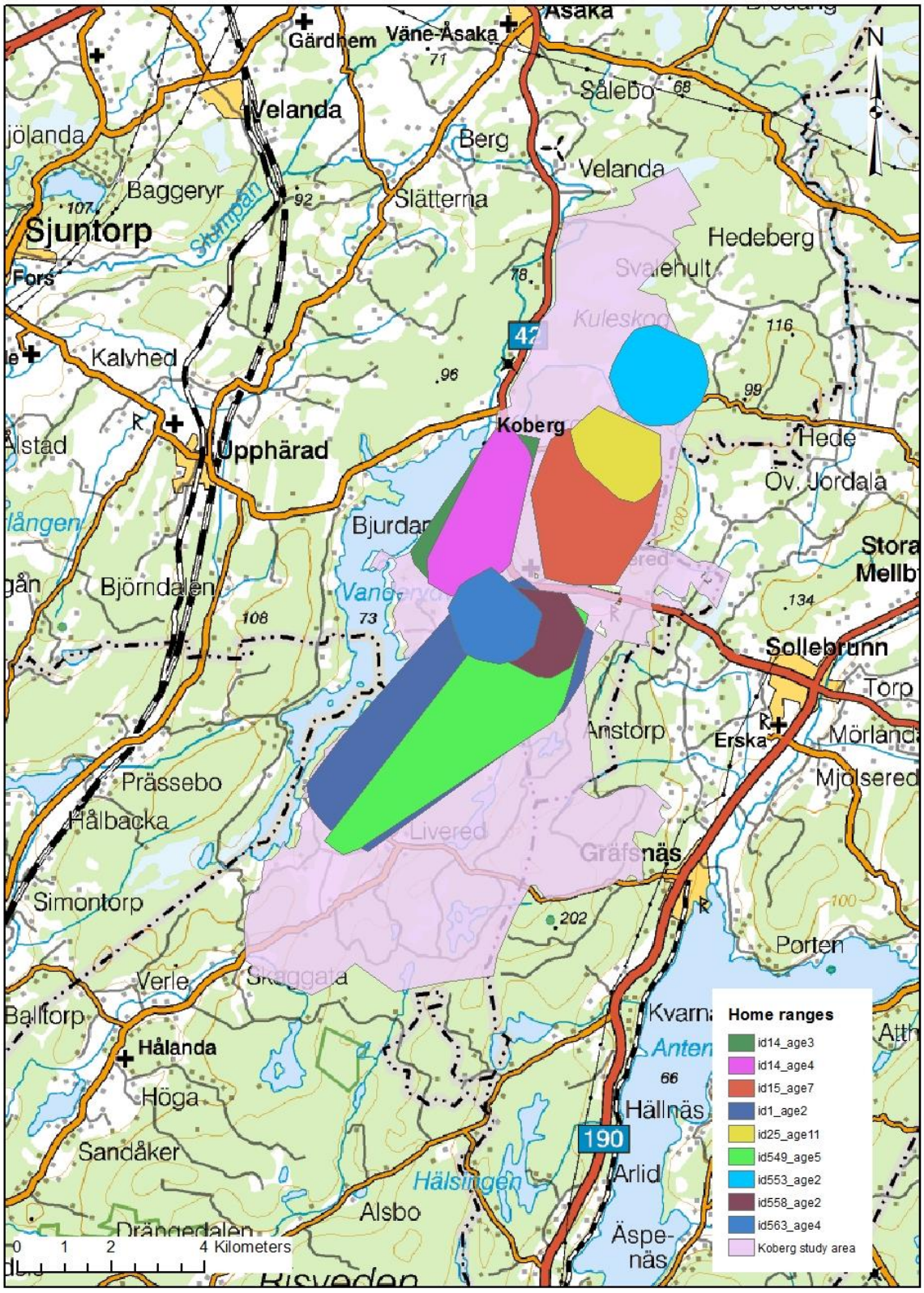

NSD for ID-565 at age 6
Net squared displacement
0e+00
2e+06
1 Sep
1okt
Date


NSD for ID-54 at age 6
Net squared displacement
0e+00
3e+06
1 Sep
1okt
1 Nov
Date

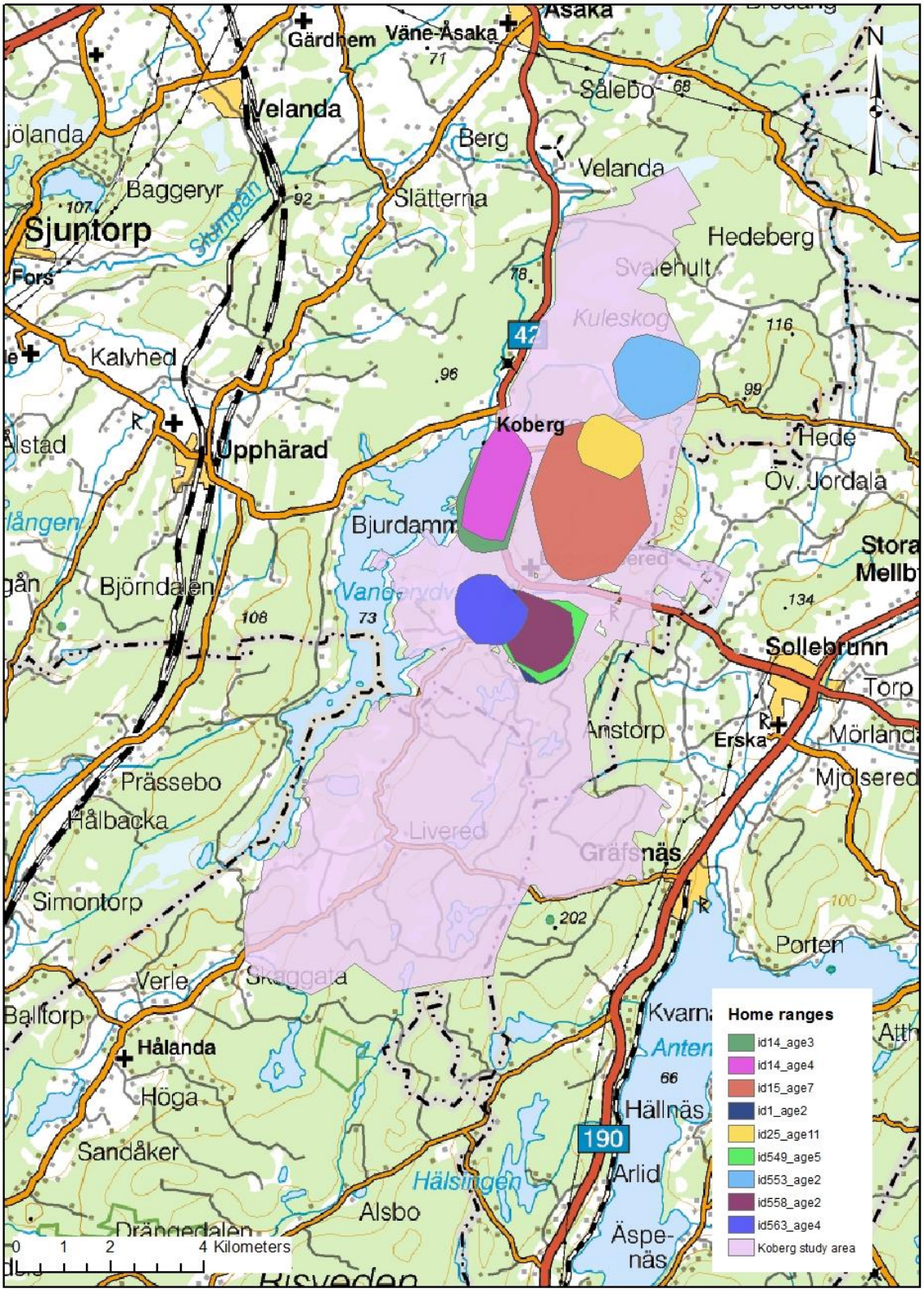

NSD for ID-31 at age 3
Net squared displacement
0e+00
6e+06
1 Sep
1okt
1 Nov
Date


NSD for ID-53 at age 3
Net squared displacement
0e+00
3e+06
1 Sep
1okt
1 Nov
Date

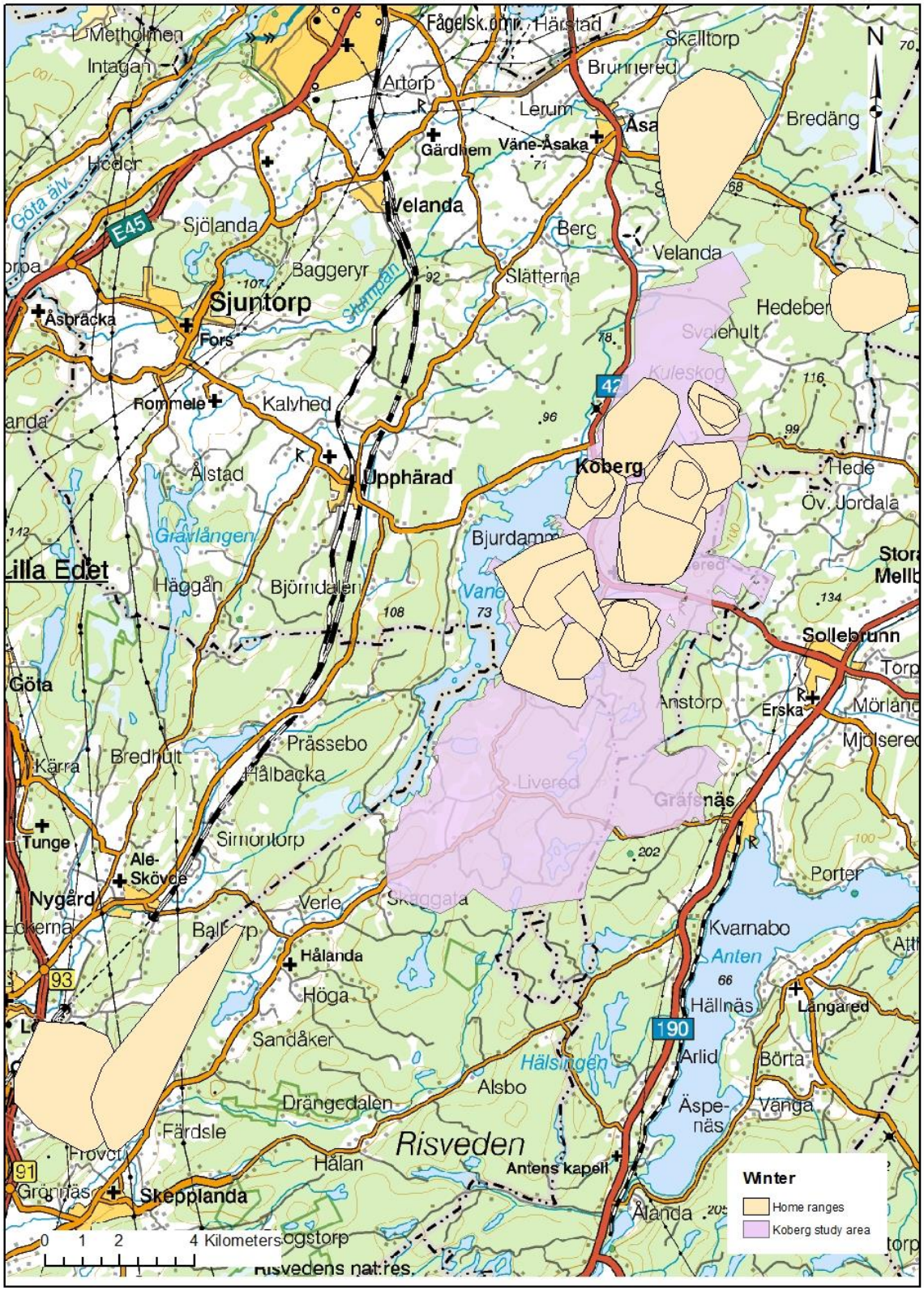
Appendix 2. Maps of home ranges.



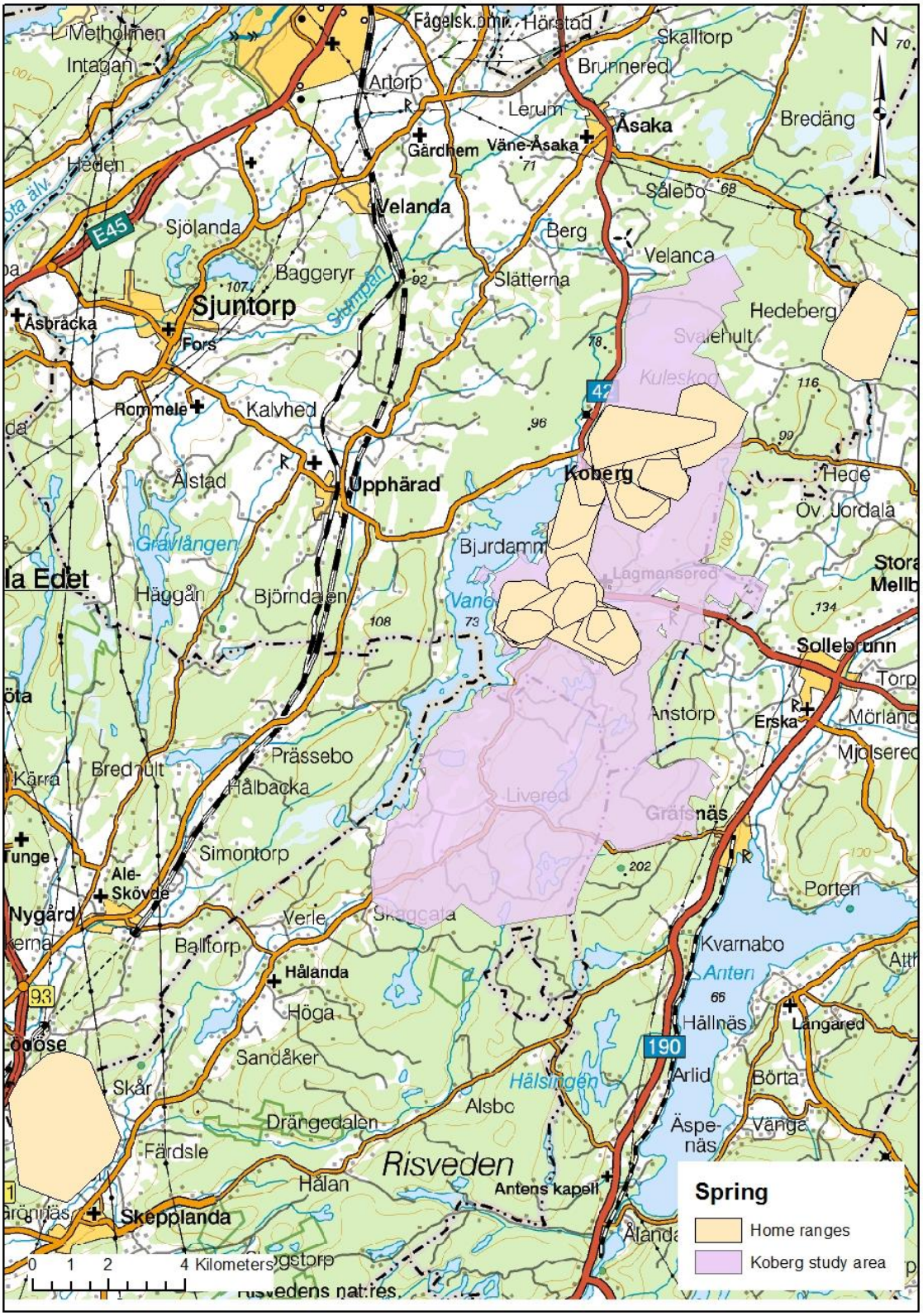
Annual and individual home range sizes with rut included for male fallow deer at Koberg estate, Sweden.



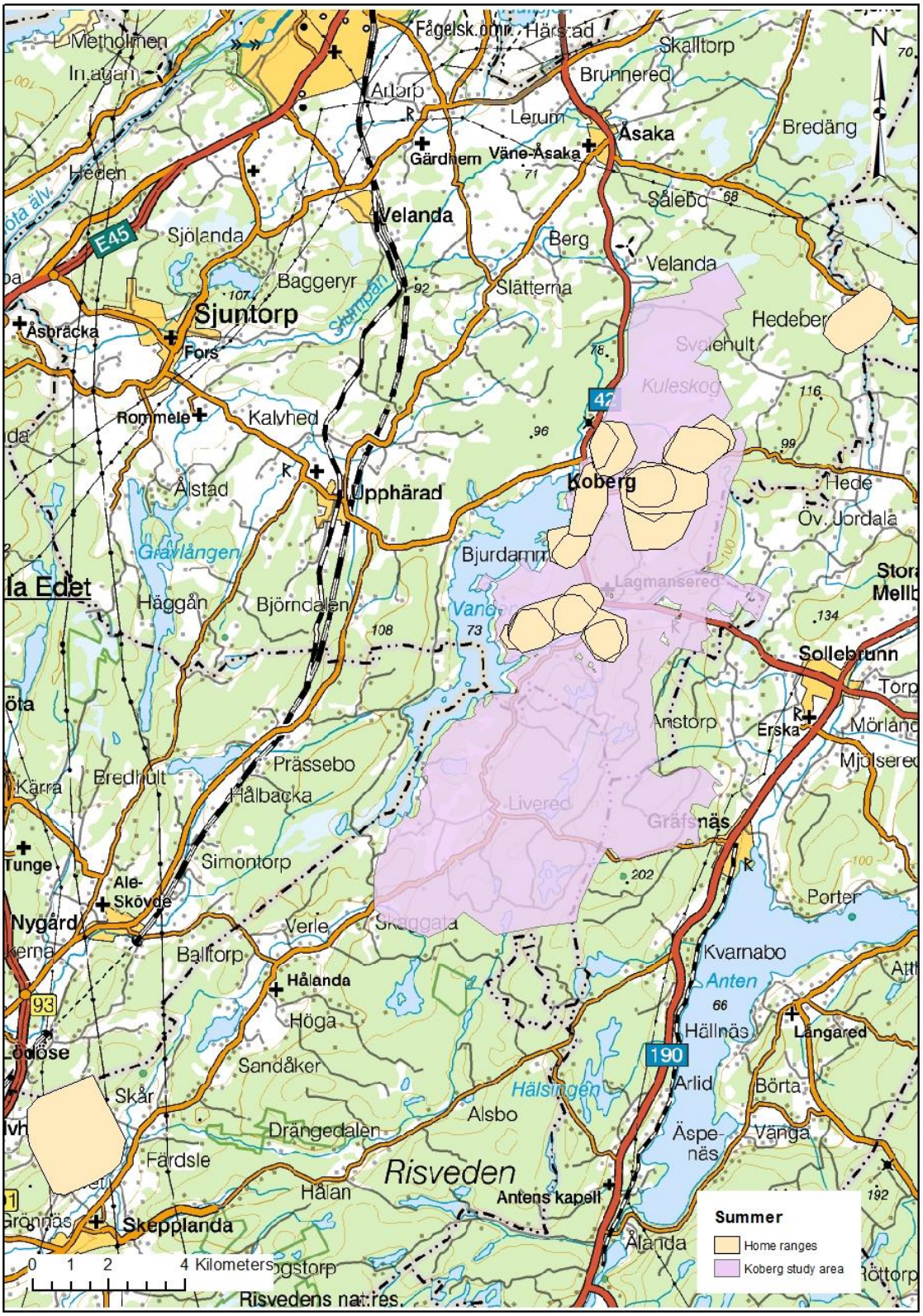
Annual and individual home range sizes with rut excluded for male fallow deer at Koberg estate, Sweden.



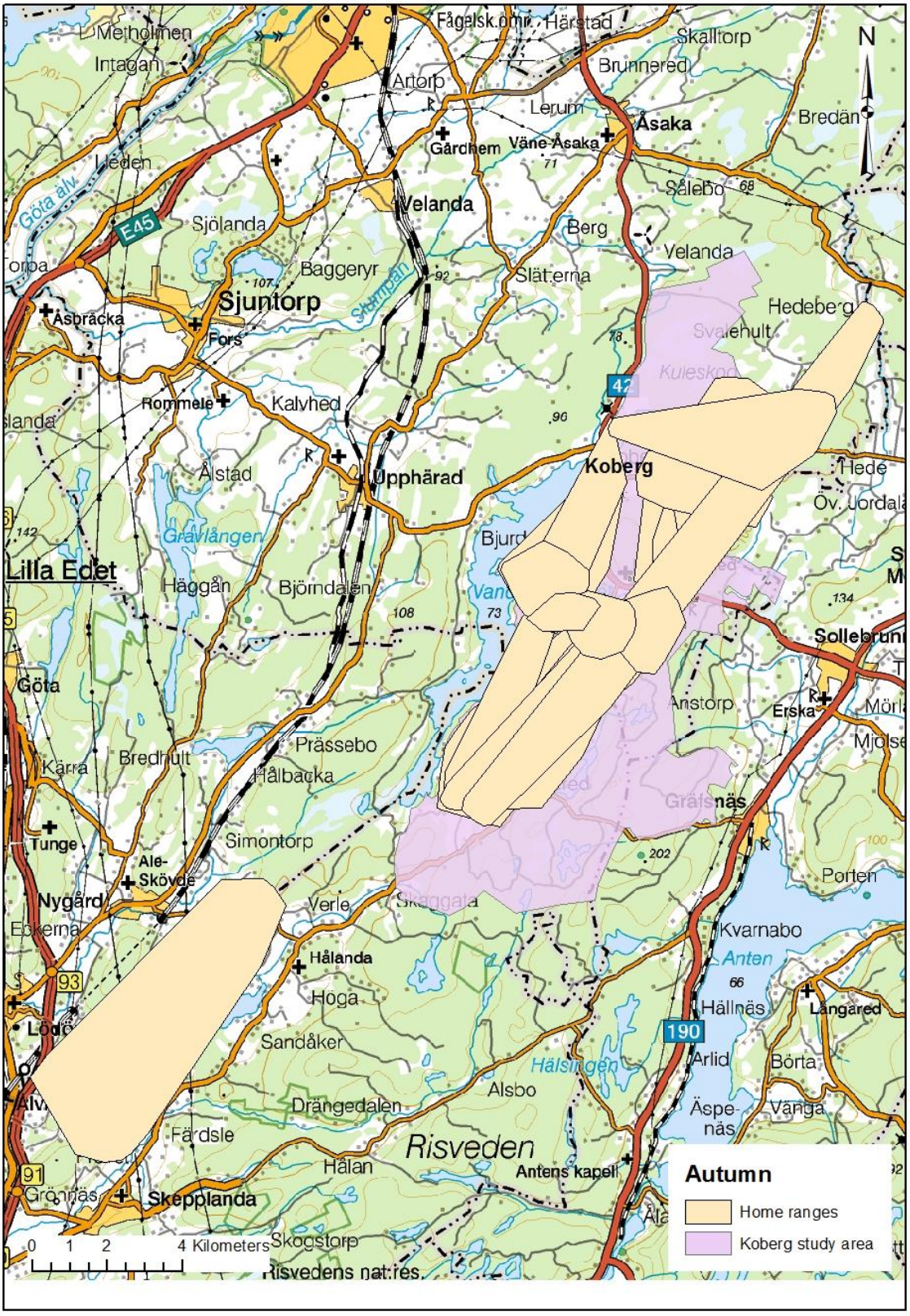
Winter home range sizes of male fallow deer at Koberg estate, Sweden. Some males are represented at several seasons in different years and ages.



Spring home range sizes of male fallow deer at Koberg estate, Sweden. Some males are represented at several seasons in different years and ages.



Summer home range sizes of male fallow deer at Koberg estate, Sweden. Some males are represented at several seasons in different years and ages.



Autumn home range sizes of male fallow deer at Koberg estate, Sweden. Some males are represented at several seasons in different years and ages.